

MOVEMENT OF MOJAVE DESERT SPARROW FLOCKS

JOHN EICHINGER AND DAVID J. MORIARTY

Cody (1971) attributed nonrandom movement in bird flocks in the Mojave Desert to selective benefits from increased foraging efficiency. By intensive nonrandom searching in a group, birds increase the patchiness of their food, making it easier for them to find previously unforaged areas and to avoid depleted areas (Cody 1971). Although evidence suggests that flocking improves foraging efficiency in birds (Moriarty 1976, 1977; Morse 1977), the general applicability of Cody's observations on desert sparrow flocks remains largely untested (see Morse 1980:276). In this study, we examined the movement of sparrow flocks in the Mojave Desert in an attempt to replicate Cody's observations. We also studied the movement patterns of water courses (e.g., washes, arroyos) because our observations indicated that the flocks might be following these topographical features. If flocks follow water courses and water moves nonrandomly, then nonrandom flock movements may not be the result of selection as described by Cody (1971), but rather a result of the terrain through which the flocks move.

METHODS

The study area was approximately 25 km S of Barstow, San Bernardino County, California, at an elevation of 653 m. The site is dominated by a central ridge with a bajada sloping gently away from the ridge to the north and the south. The terrain is broken up by occasional washes and arroyos. Perennial vegetation is dominated by creosote (*Larrea tridentata*) with some Mojave yucca (*Yucca schidigera*) and Joshua tree (*Yucca brevifolia*) present on the south slope.

Observations on flocks were made from January 1979 to March 1979 and from December 1979 to March 1980 at various times during the day. Twenty-four flocks were observed for a total of 1213 min. A flock was defined as a cohesive group of individuals moving together and reacting to social cues from one another (Moriarty 1976, Morse 1980). Typically, flocks moved in short flights between feeding sites. Data taken on each flock included: (1) flock size and composition—the estimated total number of individuals and species; (2) flock velocity—the rate of movement as estimated by the total distance moved during the total time observed; (3) time at feeding sites—the average time spent at feeding sites while the flock was observed; (4) distance between feeding sites—average distance of all straight-line flight segments between feeding sites; and (5) path directionality—estimates of the tendency for flocks to turn in various directions (explained below). To determine path directionality, we followed each flock at a distance of 40–70 m, a distance at which the birds did not appear to be disturbed. Care was taken not to flush or “drive” the flock. All distances were paced or estimated by a single observer (JE).

Path directionality involved mapping the progress of each flock. When the flock left a feeding site, the angle (to the nearest 10°) to the next feeding site was estimated using a compass. These maps were later used to score directionality between two straight sections

of path. The probability of a flock moving forward, backward, right, or left was calculated by dividing the path directionality score for that direction by the total of all path directionality scores for the flocks.

For example, suppose a flock is followed through three feeding sites, designated A, B, and C in the order visited. Further suppose that the angle between A and B is 110° (from north) and the angle between B and C is 90° . The turn at point B is scored in the following manner. The flock turned at an angle of 20° ($110^\circ - 90^\circ = 20^\circ$) when leaving site B resulting in a score of 20 to the left. As the turn was in the left, forward quadrant, and the turn was 20° to the left, the remainder of the direction in the quadrant ($90^\circ - 20^\circ = 70^\circ$) results in a score of 70 to the forward direction. This method is the same as that used by Cody (1971) except that Cody assigned a score of 90 to forward each time a straight section of path passed a 100-ft mark. We did not score any additional forward movement and scored only turns to avoid bias in favor of the forward direction.

In order to determine if water courses move in a nonrandom manner, we measured the directionality of water courses by the same method used for the bird flocks. We selected 12 water courses by starting in the middle of the study site and moving in the four cardinal directions. The first three obvious water courses (arroyos or washes) encountered in each direction were measured. Because water courses did not have "feeding sites," we defined seven functional sites at a distance of 42 m apart and measured directionality as explained above. We used seven sites at 42 m because these were the averages for these variables in the 24 flocks.

Tests for significant differences between two sample means were done using the t' procedure (Sokal and Rohlf 1969). Equality of more than two means was tested using analysis of variance. Multiple comparisons were accomplished by two-sample t -tests using Bonferroni probabilities. All directional probabilities were arcsin-transformed before statistical testing.

RESULTS

Birds observed in flocks included the resident Black-throated Sparrow (*Amphispiza bilineata*) as well as wintering Sage (*A. belli*) and White-crowned (*Zonotrichia leucophrys*) sparrows. Twelve of 24 flocks observed during the two seasons were comprised of a single species. Sage Sparrows comprised eight of the single-species flocks, White-crowned Sparrows comprised three, and Black-throated Sparrows comprised one. Sage and Black-throated sparrows were involved in seven two-species flocks. Sage and White-crowned sparrows were in one flock together. Black-throated and White-crowned sparrows were in one flock together. All of the single-species flocks were seen during the 1980 field season.

Flocks progressed in a rolling motion from one feeding site to the next with 1-3 individuals (usually Sage or Black-throated sparrows) leading the group. Feeding sites for an entire flock were usually no larger than 100 m^2 . Separate flocks were never observed intermingling.

If the directional movement of flocks was random, we would expect equal probabilities for forward, backward, right, and left turns. Average probabilities for the four directions (Table 1) were not equal ($F = 82.3$, $df = 3,92$, $P < 0.0001$). Multiple comparisons analysis indicated that the

TABLE 1
CHARACTERISTICS OF FLOCKS OF BIRDS AND WATER COURSES ON THE MOJAVE DESERT

	Flocks		Water courses
	This study N = 24	Cody (1971) N = 14	This study N = 12
No. species	1.7 ± 0.8	3.2 ± 0.9	
No. individuals	18.8 ± 10	68.0 ± 40	
Flock movement			
Velocity (m/min)			
Forward	0.10 ± 0.04	0.09 ± 0.02	0.85 ± 0.03
Right	0.61 ± 0.21	0.69 ± 0.13	0.07 ± 0.03
Left	0.20 ± 0.15	0.15 ± 0.09	0.08 ± 0.03
Reverse	0.18 ± 0.13	0.13 ± 0.07	
	0.02 ± 0.04	0.03 ± 0.04	

probability of moving forward was the largest, that there was no significant difference between the probabilities of turning right or left, and that the probability of reversing was the smallest. Flocks showed a definite tendency to move in a forward direction.

Comparison with Cody (1971).—Our study site was located about 130 km to the southeast of Cody's (1971). Both areas were in the Mojave Desert, and vegetation and topography appeared to be similar. The principal difference between the two studies is the size and composition of the flocks studied (Table 1). Flocks in our study had fewer species and individuals than did the flocks Cody observed, and his flocks varied more in the number of individuals, although coefficients of variation are similar.

There was no significant difference between flocks we observed and those observed by Cody in the velocity at which they moved (Table 1). All of the directional probabilities were the same for flocks we observed and those reported by Cody (Table 1). An analysis of variance of Cody's probabilities showed significant differences ($F = 197.7$, $df = 3,52$, $P < 0.0001$) among the means for the four directions. Multiple comparisons indicated that the forward probability was the largest, that there was no difference between the left and right probabilities, and that the probability of reversing was the smallest. In other words, although our flocks were smaller than Cody's their movement patterns were similar.

Comparison to water courses.—The probability of water courses moving forward (Table 1) was greater than the probability of our flocks moving forward ($t' = 5.5$, $P < 0.01$), while the probability of water courses going left or right (Table 1) was less than the probability of our flocks turning left or right (left, $t' = 3.6$, $P < 0.05$; right, $t' = 4.1$, $P < 0.05$). Water

courses never reversed (Table 1). The probability of our flocks turning back was significantly different from zero ($t' = 2.4$, $P < 0.05$).

Analysis of variance and multiple comparisons on water course probabilities resulted in the same pattern seen in our and Cody's flocks, i.e., the means for the three directions (reverse was excluded because there were no reversals) were significantly different ($F = 2070.9$, $df = 2,33$, $P < 0.0001$). Forward had the highest probability with no difference between left and right probabilities. The probabilities for forward, left, and right were significantly different from zero, the only value that can be assigned to the probability of water courses turning back.

DISCUSSION

Water course directionality is similar to flock movement, i.e., predominately forward with no difference between left and right turns, and reverse movement being very rare. The higher probability for movement ahead and lower probabilities of left and right turns for water courses as compared to flocks are likely a result of the greater degree of freedom of movement in birds. Although water courses are completely constrained by topography and gravity, birds have considerably more flexibility. Even if they generally follow a water course, flocks may move from course to course. While standing in one wash we could often see another wash easily, and if a flock "switched" washes it could result in a substantial turn, perhaps even a reverse movement. Therefore, although the exact probabilities of turns are different, we conclude that the overall pattern of sparrow flock movement is very similar to that of water courses. We suggest that sparrow flocks generally move forward, occasionally to the left or right, and rarely reverse, because they follow major features of local topography.

The distribution of seeds and shrubs is probably influenced by water flow (Brown et al. 1979), and following water courses may be the simplest way for birds to find these resources. We agree with Cody (1971, 1974) that flocks tend to avoid crossing over their own paths. We disagree that this movement is the result of selection for optimization behavior, and we offer the alternative explanation that the movement is a natural consequence of following the local terrain. We base this conclusion on our observations of flocks and on our data showing that the pattern of water course directionality is similar to flock movement directionality.

Even if flocks move nonrandomly because they follow water courses, it is unclear why birds should join flocks rather than forage alone. We suggest that predation rather than return-time regulation may explain the tendency of desert birds to flock. Cody (1971) dismissed predation as a factor influencing flock formation because he never saw a flock attacked. American Kestrels (*Falco sparverius*) and Golden Eagles (*Aquila chry-*

aetos) were the only avian predators present in Cody's study, and he felt it unlikely that they would attempt to take a sparrow-sized bird. We believe that predation should not be dismissed. American Kestrels have been observed taking flocking Brewer's Sparrows (*Spizella breweri*) in Arizona (M. Marshall, pers. comm.), and their diet often includes small birds (Bent 1938, Craighead and Craighead 1956). We regularly saw Loggerhead Shrikes (*Lanius ludovicianus*) on our study area, and their diet often includes small birds (Bent 1950). Reynolds (1979) observed two successful kills each of Brewer's and Sage sparrows by Loggerhead Shrikes, as well as 23 unsuccessful attempts on these species within two years in Idaho. We observed a Prairie Falcon (*Falco mexicanus*), a predator not mentioned by Cody (1971), unsuccessfully attack a flock of eight Sage and Black-throated sparrows. Caraco (1979) demonstrated that flocking Yellow-eyed Juncos (*Junco phaeonotus*) scan less often for predators and increase foraging rate as flock size increases.

Although the frequency of attempted acts of predation may be small, nevertheless they may have played an important part in the development of flocking behavior through evolutionary time. Flocks may detect predators earlier than individuals (Powell 1974, Siegfried and Underhill 1975), as well as provide a place for individuals to hide (Hamilton 1971) and confuse the predator (Powell 1974). The tendency for flocks not to form in years of abundant resources (Cody 1971) might also be predator related, as exposure to predators would be reduced when less time was spent searching for food.

SUMMARY

The movement of 24 sparrow flocks on the Mojave Desert during two winters (1979–1980) was studied. The average flock had 19 birds of two species. Flocks moved nonrandomly with a definite preference for the forward direction. Left and right turns occurred with the same frequency, and reversals were rare. A comparison with Cody's data (1971) indicated that although our flocks were significantly smaller and contained fewer species, they were identical to his in all aspects of movement. We measured the paths of water courses (washes and arroyos) by methods similar to those used to measure flock movement. Water courses show a similar pattern of movement, i.e., most often forward, followed by right and left turns at equal frequency. Water courses did not reverse. Flocks we observed appeared to follow water courses. We conclude that flocks tend to follow water courses.

We suggest that Mojave Desert sparrow flocks form in response to predator pressure and move in nonrandom paths because they follow local topography. We feel flocking may result in increased foraging efficiency, but that it is not necessary to invoke complex optimization models (Cody 1971, 1974) to explain their formation and behavior.

ACKNOWLEDGMENTS

We thank J. Rotenberry and several anonymous reviewers for helpful criticisms of the original manuscript. Thanks to M. Marshall for encouragement and for sharing observations on sparrows.

LITERATURE CITED

- BENT, A. C. 1938. Life histories of North American birds of prey, Pt. 2. U.S. Natl. Mus. Bull. 167, Washington, D.C.
- . 1950. Life histories of North American wagtails, shrikes, vireos, and their allies. U.S. Natl. Mus. Bull. 197, Washington, D.C.
- BROWN, J. H., O. J. REICHMAN, AND D. W. DAVIDSON. 1979. Granivory in desert ecosystems. *Ann. Rev. Ecol. Syst.* 10:201-227.
- CARACO, T. 1979. Time budgeting and group size: a test of theory. *Ecology* 60:618-627.
- CODY, M. L. 1971. Finch flocks in the Mohave Desert. *Theor. Pop. Biol.* 2:142-158.
- . 1974. Optimization in ecology. *Science* 183:1156-1164.
- CRAIGHEAD, J. J. AND F. C. CRAIGHEAD. 1956. Hawks, owls and wildlife. The Stackpole Co., Harrisburg, Pennsylvania.
- HAMILTON, W. D. 1971. Geometry for the selfish herd. *J. Theor. Biol.* 31:295-311.
- MORIARTY, D. J. 1976. The adaptive nature of bird flocks: A review. *Biologist* 58:67-79.
- . 1977. Flocking and foraging in the Scarlet-rumped Tanager. *Wilson Bull.* 89:151-153.
- MORSE, D. H. 1977. Feeding behavior and predator avoidance in heterospecific groups. *Bioscience* 27:332-339.
- . 1980. Behavioral mechanisms in ecology. Harvard Univ. Press, Cambridge, Massachusetts.
- POWELL, G. V. N. 1974. Experimental analysis of the social value of flocking by starlings (*Sturnus vulgaris*) in relation to predation and foraging. *Anim. Behav.* 22:501-505.
- REYNOLDS, T. D. 1979. The impact of Loggerhead Shrikes on nesting birds in a sagebrush environment. *Auk* 96:798-800.
- SIEGFRIED, W. R. AND L. G. UNDERHILL. 1975. Flocking as an anti-predator strategy in doves. *Anim. Behav.* 23:504-508.
- SOKAL, R. R. AND F. J. ROHLF. 1969. Biometry. W. H. Freeman and Co., San Francisco, California.

BIOL. SCI. DEPT., CALIFORNIA STATE POLYTECHNIC UNIV., POMONA, CALIFORNIA 91768. ACCEPTED 10 OCT. 1984.